Climate change and reseeding shape richness-evenness relationships in a subalpine grassland experiment

Lina K. Mühlbauer[1], * (ORCID: 0000-0002-6493-2742)

Andreas Klingler[2]

Lukas Gaier[2]

Andreas Schaumberger[2]

Adam Thomas Clark[1] (ORCID: 0000-0002-8843-3278)

*Author to whom correspondence should be addressed: lina.muehlbauer@uni-graz.at

1 Institute of Biology, University of Graz, Holteigasse 6, 8010 Graz, Austria

2 Agricultural Research and Education Centre (AREC) Raumberg-Gumpenstein, Raumberg 38, 8952 Irdning-Donnersbachtal, Austria

Key words: climate change; grassland; evenness; richness-evenness relationship; management; community responses

Abstract

1. Grasslands face an uncertain future due to climate change. Although there is increased interest in the interdependencies of different biodiversity components, the effects of climate change on these relationships remain understudied. One of these is the richness-evenness relationship (RER), which is sensitive to altered species abundances in relation to richness. This relationship may be important as evenness and richness jointly shape diverse ecosystem functions, such as stability and productivity. As evenness affects productivity differently in low and high richness communities, the richness-evenness relationship is important to investigate, especially under climate change.

2. Here, we assess the effects of increased CO_2 concentrations, temperature, and drought on the RER in a subalpine long-term (2010 - ongoing) grassland climate change experiment, and test whether these effects can be buffered by reseeding. We provide evidence that climate change alters the RER in our experiment, and that these changes occur independently of changes in richness and evenness separately. Reseeding erases the differences in RER between treatments and controls but fails to restore the negative RER initially found in controls. Further, we show that the dominant grass species in our system *(Arrhenatherum elatius)* responds differently to each climate change factor, with opposite effects in high vs. low richness plots, thereby largely determining the direction of the RER.

3. These results suggest that the RER can reveal additional insights on community responses to climate change and represents a different signal than evenness or richness alone. A more nuanced approach integrating evenness and maximizing richness in seed mixtures could be an important step forward to better match restoration treatments to particular community types and global change drivers.

Introduction

Grasslands face an uncertain future due to climate change (Stevens et al. 2022). Climate change experiments suggest that biodiversity, productivity, and stability can be altered by increased temperature levels (Kardol et al. 2010; Wang et al. 2020; Fussmann et al. 2014), but elevation of CO_2 concentrations could potentially ameliorate these effects (Reyes-Fox et al. 2014; Roy et al. 2016). Overall, warming seems to decrease richness and slightly also evenness, probably due to heat-tolerant species increasing in cover and susceptible species disappearing. An increase in atmospheric CO_2 alters resource and water availability in the soil and therefore changes the competitive interactions between plant species. Consequently, the response to CO_2 is suggested to be largely mediated by species identity (Niklaus et al., 2001, Potvin et al. 2007; Navas et al. 2002; Ramsier et al. 2005). In natural communities, CO_2 seems to have no effect on species richness, but enhances species evenness in an experiment in the Swiss Alps (Niklaus et al., 2001). In a field experiment in Quebec in a less species-rich community, species loss and increases in species evenness were reported (Potvin and Vasseur 1997). Also, elevated CO_2 seems to reduce species loss driven by nitrogen addition, at least in low richness communities (Reich, 2009).

While many studies have quantified the effects of increased temperature and CO_2 separately, evidence from controlled experimental settings with interactive effects is rarer, but they seem to range from simple and additive to highly complex interactions (Stevens et al. 2022). In most studies in temperate regions, species richness remains unchanged or even increases, while evenness decreases (Kardol et al. 2010; Liu et al. 2018) when grasslands are exposed to enhanced temperatures and CO_2 concentrations. On the other hand, some studies suggest a dramatic loss of species richness (Zavaleta et al. 2003). Drought impact is expected to result in species loss, either through heat stress (Klein et al. 2004) or decreased soil moisture (White et al. 2014). In general, in grassland climate change experiments, biodiversity responses differ widely, especially depending on region (Bütof et al. 2012). This is especially true for drought responses, where the local climate and ecosystem properties, like community composition, determine the magnitude of drought effects (Isbell et al. 2015; Boeck et al. 2016; Gruner et al. 2017), and nutrient addition can amplify the impacts of drought (van Sundert et al. 2021). Additionally, biodiversity

3

93   responses seem to lag behind to effects of climate change, especially in

94   mountainous regions (Alexander et al. 2018; Rumpf et al. 2019).

95   Although there is increased interest in the interdependencies of different biodiversity

96   components (e.g. Blowes et al. 2022) and the effects of climate change on the

97   relationships between different biodiversity components remain understudied. One

98   example of these interdependencies is the relationship between species richness

99   and evenness over several communities, known as the "richness-evenness

100   relationship" (RER). The RER could be an early sign of community changes, evident

101   long before serious impacts such as extinction events take place, as proposed for

102   evenness (Chapin et al. 2000). As the RER has been shown to vary in space, time,

103   and across environmental conditions or trophic levels (Soininen et al. 2012; Zhang et

104   al. 2012), a change in RER is likely an important indicator of underlying biological

105   processes. Also, evenness and richness jointly shape diverse ecosystem functions,

106   like productivity (e.g., Clare et al. 2022), as well as the stability of ecosystems

107   (Wang et al. 2021).

108   Recently, Hordijk et al. (2023) were able to show that evenness mediates the global

109   species richness- productivity relationship, such that at high species richness, even

110   communities are more productive than uneven ones, whereas the contrary is true for

111   low richness systems. This finding emphasizes the importance of investigating the

112   relationship of evenness and richness, as changes in the relationship could indicate

113   that less productive communities (low richness, high evenness and high richness,

114   low evenness) get replaced by more productive communities (low richness, low

115   evenness and high richness, high evenness) (Fig. 1, b). Stirling and Wilsey (2001)

116   conducted regression analyses of published data on the relation between evenness

117   and species richness and concluded that the RER is mostly positive in animals and

118   negative in plants and fungi, while more comprehensive analyses are still missing. Of

119   major importance in analyzing the RER is that many of the commonly used

120   evenness metrics (such as Shannon's or Pielou´s evenness) are mathematically

121   constrained by species richness, such that they necessarily increase or decrease

122   with richness, independent of any variation in species composition (Smith und

123   Wilson 1996; Tuomisto, 2012; Hordijk et al. 2023). As we examine richness-

124   evenness relationships, the most important feature for an evenness metric in our

125   analysis is species richness-independence – in other words, an effective evenness

126   metric should be able to span its full range of possible values at any level of species

4

127 richness. Studies investigating RERs use species richness independent evenness

128 metrics (e.g., Hordijk et al., 2023) and evenness metrics that are constrained by

129 species richness (e.g., Soininen et al., 2012). Here, we use the unbiased Gini

130 coefficient (Lorenz 1905) commonly used to assess inequality in economics, which

131 has been shown in previous studies to be a robust, species richness-independent

132 evenness metric (Chao und Ricotta 2019).

133 In addition to the assessment of climate change effects on biodiversity, the mitigation

134 of these effects increases in importance. Temperate grasslands in Europe contain

135 the most diverse plant communities in Europe (WallisDeVries et al. 2002). Besides

136 their biodiversity, European grasslands are economically important as a source of

137 fodder, and, to a lesser extent, fiber, and energy. Consequently, central European

138 grasslands are often intensively fertilized and mowed up to 6 times a year.

139 Intensively managed permanent agricultural grasslands are less diverse than

140 extensively managed grasslands, with lower mowing frequencies and fertilizer

141 application, but account for 34% of agriculturally used land in Europe (Eurostat

142 2020). Understanding the effects of climate change and investigating potential

143 restoration strategies is therefore particularly relevant in these agricultural

144 grasslands, due to the wide range of services and economic benefits they provide.

145 In grasslands, the most common restoration method is reseeding, independent of the

146 kind of disturbance. There is also evidence that passive restoration, i.e. the recovery

147 of natural grasslands without additional actions like reseeding, fails to completely

148 restore biodiversity (Ladouceur et al. 2023). Evidence for the results of reseeding as

149 a restoration strategy is mixed but has thus far been assessed primarily for soil

150 properties, phenology, and productivity (Zhu et al., 2020; Wang et al., 2020).

151 How reseeding affects different facets of biodiversity, and their interdependencies, is

152 often not assessed, as most conservation studies concentrate on boosting rare

153 species abundances (Samson and Knopf 1994) or focus on creating or restoring

154 species-rich, extensively used grasslands (Slodowicz et al. 2023). Therefore, an

155 open and important question is whether and how 1) climate change affects the

156 relationship between evenness and richness (RER) and 2) if reseeding can erase, or

157 at least partially alleviate, these effects in intensively used grasslands.

158 Here, we test the effects of increased CO_2 concentrations, temperature, and drought

159 interactively on richness and evenness and on the RER in a unique subalpine,

160 agricultural long-term (2010 - ongoing) climate change experiment and assess the

161   effects of reseeding under climate change. We expect an increase in species

162   richness and evenness with higher CO_2 levels, as CO_2 could ameliorate the effects

163   of fertilization in the nutrient-rich grasslands in our experiment and enable less

164   competitive species to colonize. The increase in temperature could lead to

165   decreased richness and evenness, due to heat stress or decreased water

166   availability. Simultaneous increase of CO_2 and temperature would lead to unchanged

167   evenness and richness, as CO_2 could ameliorate the effects of temperature due to

168   reduced evapotranspiration, thereby buffering the effects of increased temperature

169   (Veronika Slawitsch et al. 2019). With additional drought application, we expect

170   species richness and evenness to decrease, as water and heat stress increase and

171   are too high to be buffered by CO_2 and therefore reduced evapotranspiration (Fig. 1,

172   a). Changes in species evenness alone lead to no changes in the RER, while the

173   effect of species richness changes (addition or removal of species) depends on the

174   abundance of the respective species. If a treatment leads to increased evenness and

175   richness, we expect no change in RER if the added species is common, but if a rare

176   species is added, we expect the RER to become positive (Fig. 1, c.). On the

177   contrary, if a treatment is expected to decrease evenness and richness, we expect

178   changes in the steepness of the slope, but no change in the direction of the RER.

179   We expect a change in direction of RER by reseeding, if low richness, high evenness

180   plots are reseeded, several new species can establish, leading to an increase in

181   richness and consistent evenness. In contrast, when high-richness, low evenness

182   plots are reseeded with a mixture containing a large amount of the already dominant

183   species, the dominant species can competitively suppress other species in the

184   mixture, thereby leading to decreased richness and slightly decreased evenness.

185   This leads to positive RER (Fig. 1, b. and e.). Additionally, we expect the RER to

186   change independently from changes in richness and evenness separately (Fig. 1, f.).

187   These changes, i.e. the replacement of low richness, high evenness (LRHE) and

188   high richness, low evenness communities (HRLE) by low richness, low evenness

189   (LRLE) and high richness, high evenness (HRHE) communities have consequences

190   for productivity and stability and underline the importance of investigating the effects

191   of climate change not only on species richness and evenness, but also on their

192   relationship.

193

a.

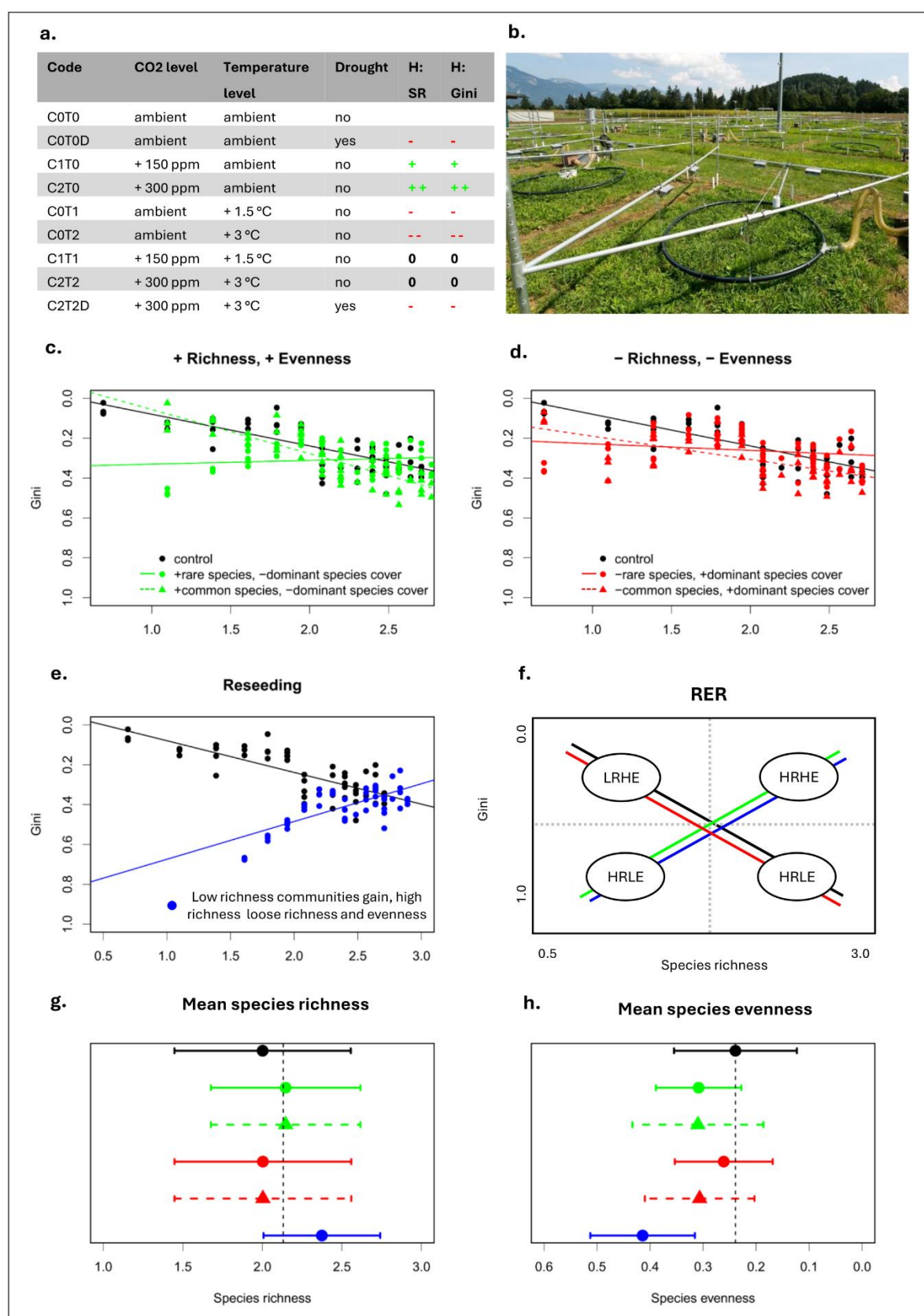| Code	CO2 level	Temperature level	Drought	H: SR	H: Gini
C0T0	ambient	ambient	no		
C0T0D	ambient	ambient	yes	-	-
C1T0	+ 150 ppm	ambient	no	+	+
C2T0	+ 300 ppm	ambient	no	+ +	+ +
C0T1	ambient	+ 1.5 °C	no	-	-
C0T2	ambient	+ 3 °C	no	- -	- -
C1T1	+ 150 ppm	+ 1.5 °C	no	0	0
C2T2	+ 300 ppm	+ 3 °C	no	0	0
C2T2D	+ 300 ppm	+ 3 °C	yes	-	-

Figure 1: Conceptual figure showing hypotheses of potential kinds of biodiversity change, and their corresponding potential impacts on the RER in response to climate change (increase in CO_2, temperature, and drought via rainout shelter) and reseeding based on

7

198   simulated data (see Methods). Hypotheses for the effects on evenness and richness

199   separately for each treatment (a., g., and h.) and their combined effect on RER (c., d., and

200   e.) are shown. Colors indicate expected changes in biodiversity due to experimental

201   treatments. Green indicates increases and red decreases in richness and evenness

202   simultaneously**.** Black indicates control plots. We expect an increased species richness and

203   evenness with higher CO_2 concentrations, but an unchanged relationship between evenness

204   and richness. The temperature treatment could lead to decreased richness and evenness,

205   due to heat stress and reduced water availability. Simultaneous increase of CO_2 and

206   temperature could lead to unchanged evenness and richness and a negative RER, as CO_2

207   could ameliorate the effects of temperature. With additional drought application, we expect

208   species richness and evenness to decrease, as water and heat stress increase and are too

209   high to be buffered by CO_2 and therefore reduced evapotranspiration (**a.**). We expect no

210   change in the direction of RER, as we expect the treatments to affect low and high richness

211   communities in the same way. In controls, we expect higher diversity plots also tend to be

212   dominated by a single abundant species (red triangles), with less abundance in low diversity

213   plots leading to low evenness, as observed for natural plant communities and consequently

214   to a negative RER (**c., d., e., and f.**). We expect the RER to change in direction, due to

215   increases in richness and evenness, if the added species is rare, i.e., low percentage cover,

216   and due to reseeding (**c.** and **e.**). We expect no change in the direction of the RER following

217   decreases in richness and evenness, only changes in the steepness of the slope (**d).**

218   When low-richness control plots are reseeded, several new species can establish, leading to

219   an increase in richness and consistent evenness. In contrast, when high-richness plots are

220   reseeded with a mixture containing a large amount of the already dominant species, the

221   dominant species can competitively suppress other species in the mixture, thereby leading

222   to decreased richness and slightly decreased evenness and therefore a change in the

223   direction of the RER (**e.**). These changes, i.e. the replacement of low richness, high

224   evenness (LRHE) and high richness, low evenness communities (HRLE) by low richness,

225   low evenness (LRLE) and high richness, high evenness (HRHE) communities has

226   consequences for productivity and stability (**f.**) and are only partly detectable by changes in

227   mean (points and triangles) and standard deviation (lines) of richness and evenness

228   separately (**g.** and **h.**). In controls, higher diversity plots also tend to be dominated by a

229   single abundant species (red triangles), with less abundance in low diversity plots leading to

230   low evenness, as observed for natural plant communities. b. shows one plot of the

231   ClimGrass experiment in Raumberg-Gumpenstein, Styria, Austria (47°29'38.5" N

232   14°06'02.6" E, 732 m) after mowing, with the black fumigation ring and the heaters visible.

233   Methods (1368)

Experimental design

234

235 The *ClimGrass* climate change experiment was established at the Agricultural

236 Research and Education Centre (AREC) in Raumberg-Gumpenstein, Styria, Austria

237 (47°29'38.5" N 14°06'02.6" E, 732 m). This experiment focuses on agriculturally

238 relevant management methods (e.g., fertilization, mowing, reseeding), and because

239 of its subalpine location (Pötsch et al. 2020). With a mean annual precipitation of

240 1077 mm per year and a mean annual temperature of 8.5 °C, the location is

241 representative of most low-elevation parts of the eastern European Alps. Climate

242 diagrams for the changes in precipitation and temperature over the last decades can

243 be found in the supplement (Fig. S1). The soil is mainly brown soil with a loamy

244 texture consisting of 44.2% sand, 47.6% silt, and 8.3% clay with a mean pH of 5.7

245 (Herndl et al. 2011). The grassland was established in 2007 and seeded with the

246 *DWB* Seed mixture (see S1, Tab. 4 for details) on bare soil; the same mixture was

247 used for reseeding. The climate change treatments were started in 2010 and are still

248 ongoing. The site can be classified as a nutrient-rich meadow that primarily consists

249 of three C_3 grass species: tall oat-grass (*Arrhenatherum elatius* L.), Kentucky

250 bluegrass (*Poa pratensis* L.), and orchard grass (*Dactylis glomerata* L.), together

251 with common forbs and legumes, e.g., dandelion (*Taraxacum officinale* L.) or red

252 clover (*Trifolium pratense* L.).

253 The meadow is mowed three times per year during the growing season (April to

254 October). Mineral fertilizer is also applied three times annually, resulting in a total

255 amount of 90 kg N ha−1 y−1, 65 kg P ha−1 y−1, and 170 kg K ha−1 y-1 (Deltedesco

256 et al. 2019). The field experiment is designed following a response surface approach

257 (Piepho et al. 2017). It consists of 54 plots with a size of 16 m^2 each. Experimental

258 treatments impose various levels of CO_2 (ambient, +150, +300 ppm; denoted by C0,

259 C1, and C2), air temperature (ambient, +1.5°, +3 °C; denoted by T0, T1 and T2), and

260 simulated drought (denoted by "D"). Interactive treatments between temperature,

261 CO_2 and drought are also implemented. The C2T2 treatment (+300 ppm and +3°C)

262 is based on the most likely future climate change scenario for the European alps

263 (Gobiet et al. 2014). All treatment descriptions can be found in Tab.1.

264 The temperature treatments are heated by six infrared radiators. The CO_2 treatments

265 are maintained by mini-FACE (Free Air Carbon Dioxide Enrichment) rings around the

266 plots, where the CO_2 concentration is controlled via a sensor in the plot center

9

267   (Herndl et al. 2011). The temperature increase is applied all year round when the

268   snow cover is below 10 cm, while CO_2 is only added during daytime in the growing

269   season. Control plots are also equipped with mini-FACE rings with ambient air flow

270   and unconnected radiators to control for shading and unintended equipment effects

271   (Herndl et al. 2011; Pötsch et al. 2020). Drought treatments with rainout shelters

272   have also been included since 2017 (Veronika Slawitsch et al. 2019). These were

273   used to simulate the effects of severe droughts, with a total reduction in incoming

274   precipitation in 2017, 2019, 2020, 2021 and 2022. To end each drought period,

275   drought treatments received 40 mm of irrigation supplied from collected rainwater,

276   manually applied to the drought plots (see S1, Tab. S7). As an agricultural

277   experiment, plots were periodically reseeded to help increase cover, after visual

278   assessment for ants, voles, or cockchafer grubs. Reseeding took place in 2018,

279   2020 and 2021, mimicking the management methods that farmers in the area would

280   have implemented. Because the reseeding mixture (see S1, Tab. S4) is identical

281   with the initial seed mixture, no new species were introduced, and relative seed

282   amounts matched those for the initial conditions of the experiment. The colonization

283   of different species could occur additionally. The number of reseeded plots per

284   treatment can be found in Tab. 1. Vegetation surveys were conducted in 2013, 2017,

285   2019 and 2022 to record species-level absolute cover in each plot. Absolute cover

286   and species richness estimates were performed in mid to end of May in the 1 m^2

287   harvest ring in the plot center (Peratoner und Pötsch 2019).

10

Data simulation

289   To better explore our hypotheses of the effects of changes in evenness and richness

290   separately on the relationship between them, we simulated species richness and

291   corresponding abundance for each species. We simulated species richness from a

292   uniform distribution between 2 and 15 species for 54 plots. We sampled the

293   percentage cover abundance for each species from a normal distribution with a

294   mean of 20% cover. To account for the negative RER found in the available literature

295   (Soininen et al., 2012; Zhang et al., 2012; Hordijk et al., 2023), we sampled the

296   abundance of plots with less than 8 species from a normal distribution with a lower

297   standard deviation of 5 %, and communities with more than 8 species with a higher

298   standard deviation of 15%. The resulting overall percentage cover was then

299   normalized to 100% cover, and Gini and species richness were calculated (see

300   Methods: Biodiversity metrics), as performed for the actual experimental survey

301   data. To add a rare species to plots, we sampled from a uniform distribution with 1 to

302   5 % cover. To remove a rare species, we removed the rarest species of the

303   community in plots with species richness greater than 2. To decrease or increase

304   evenness, we added or removed 5% cover to or from the dominant species. To

305   simulate our expectations for the biodiversity changes due to reseeding, we sampled

306   three rare species (uniform distribution; 1 to 5 % cover) to add to plots with less than

307   8 species, and added 40% cover to the dominant species.

308 ## Data analyses

309 All analyses were conducted using R 4.2.2. (R Core Team, 2022).

310 **Table 1: Analyzed treatments**, corresponding codes, number of plots, and number of
311 analyzed plots (reseeded from 2018) for each treatment.
312

Code	CO$_2$ level	Temperature level	Drought	#Plots	#Analysed (reseeded)
C0T0	ambient	ambient	no	16	13
C0T0D	ambient	ambient	yes	4	4
C1T0	+ 150 ppm	ambient	no	4	3
C2T0	+ 300 ppm	ambient	no	6	2
C0T1	ambient	+ 1.5 °C	no	4	3
C0T2	ambient	+ 3 °C	no	6	4
C1T1	+ 150 ppm	+ 1.5 °C	no	3	2
C2T2	+ 300 ppm	+ 3 °C	no	7	4
C2T2D	+ 300 ppm	+ 3 °C	yes	4	4

313

314 To prevent post-treatment bias in subsequent analyses, we only used the vegetation
315 data from plots that were reseeded in 2018, 2020, and 2021. Thus, we exclude data
316 from plots that were never reseeded (in total, 15 plots). Also, within individual
317 analyses, we used either solely data from plots that had not yet been reseeded or
318 solely data from plots that had already been reseeded (i.e., we never mixed data
319 from pre- and post-reseeding within a single analysis). All analyzed treatments and
320 the corresponding number of replicates can be found in Tab. 1.

321 ## Biodiversity metrics

322 To examine the effects of experimental treatments on RER, species richness and
323 evenness were calculated for each plot in each year. The unbiased Gini metric,
324 calculated as:

325
$$G = \frac{\sum_{i=1}^{n}(2i-n-1)x_i}{n\sum_{i=1}^{n}x_i} \tag{1}$$

326 was used to quantify the richness independent evenness (Chao and Ricotta 2019),
327 where x is the observed abundance in percentage cover of a species, n is the

12

328   number of species observed, and i is the rank of values in ascending order (Buchan,

329   2002). We did so using the R package DescTools, version 0.99.46. Before

330   calculating evenness, cover estimates were normalized to absolute (i.e., summing to

331   100 percent) cover (not counting bare ground). Importantly, note that Gini, in contrast

332   to commonly used evenness metrics (e.g., Shannon's or Pielou's evenness), ranges

333   between 0 and 1, where 0 indicates complete evenness (i.e., all species having

334   equal abundance), and 1 indicates complete dominance by a single species. For

335   easier interpretability, all evenness axes in the main figures are flipped, i.e., to

336   display 1 at the bottom of the axis and 0 at the top. To investigate differences in

337   species richness and evenness, we fit linear regressions predicting evenness and

338   log-transformed species richness as a function of treatment. We included plot as a

339   random effect, and year as a categorical fixed effect (i.e., resulting in models of the

340   form gini/species richness ~ Treatment + date_factor + (1|plot)). Differences in

341   species richness and evenness between years can be found in the supplement (Fig.

342   S6-10). All linear regressions were performed using Bayesian Generalized Linear

343   Multivariate Multilevel Models in the brms R package, version 2.17.0. We used the

344   default settings for the package, i.e., with 1000 burn-in steps, 1000 MCMC

345   optimization steps, four chains, and flat priors (Bürkner 2017). In all cases, models

346   achieved convergence, with R-hat estimates of <1.1 for all models and parameters.

347   Significant differences in species richness and evenness between treatments and

348   control were identified by comparing the posterior distributions of intercept estimates

349   across the fitted regressions.

350   ## Richness-evenness- relationships (RER)

351   To investigate differences in RER between control and treatments, we fit linear

352   regressions predicting evenness as a function of logarithmic species richness, with

353   separate regression fits for each combination of experimental treatments. Recall that

354   we analyzed only plots that were reseeded at some point in 2018, 2020, and 2021,

355   and that in all cases, we separately fit functions for the RER prior to reseeding, and

356   after reseeding. All linear regressions were performed using Bayesian Generalized

357   Linear Multivariate Multilevel Models in the brms R package, version 2.17.0. We

358   used the default settings for the package, i.e., with 1000 burn-in steps, 1000 MCMC

359   optimization steps, four chains, and flat priors. In all cases, models achieved

13

360   excellent convergence, with R-hat estimates of <1.1 for all models and parameters.

361   Survey year and treatments as factors were included as fixed effects in the models,

362   whereas plot identity was modeled as a random effect acting on the model intercept,

363   i.e., of the form (1|Plot) (Bürkner, 2017). Significant differences in the RER across

364   experimental treatments were identified by comparing the posterior distributions of

365   intercept and slope estimates across the fitted regressions.

A. elatius cover

366

367   To examine how the abundance of the dominant species *A. elatius* was associated

368   with the difference in RER before and after reseeding, we calculated the difference in

369   *A. elatius* cover before reseeding (vegetation surveys in 2013, 2017) vs. after

370   reseeding (vegetation surveys in 2019, 2022), as well as differences in species

371   richness and evenness. We then fitted regression lines for the relationship between

372   log-transformed species richness vs. evenness, with corresponding confidence

373   intervals, using brms. Log transformation was necessary to meet normality

374   assumptions for model residuals.

14

Results (1151)

Treatments increase richness and reduce evenness

In general, experimental CO_2, temperature, and drought treatments tended to increase richness and reduce evenness before reseeding, with two minor exceptions (Fig. 2, a-b). First, in the CO_2 treatments at ambient temperature levels (C1T0, C2T0), mean evenness was somewhat higher than in control plots. Second, in the +1.5 °C treatments at ambient CO_2 (C0T1), mean richness was somewhat lower than in control plots. Before reseeding, species richness was only increased in the Scenario 2 (+300 ppm, 3°C) treatment, while evenness was significantly decreased in both scenarios (C1T1: +150 ppm, 1.5°C; C2T2: +300 ppm, 3°C) (Tab. 2). The RER in the control treatment before reseeding is negative in 2013 and in 2017, whereas the differences between control and treatment RER is more pronounced in 2017 (Fig. 2, b. and c.) Therefor, we controlled for temporal variation by including year as a continuous fixed-effect predictor in regression analyses described below (Fig. 3 and 4) – recall again that all comparisons were conducted either between treatments before reseeding, or after reseeding, but never with mixed data from both time-periods.
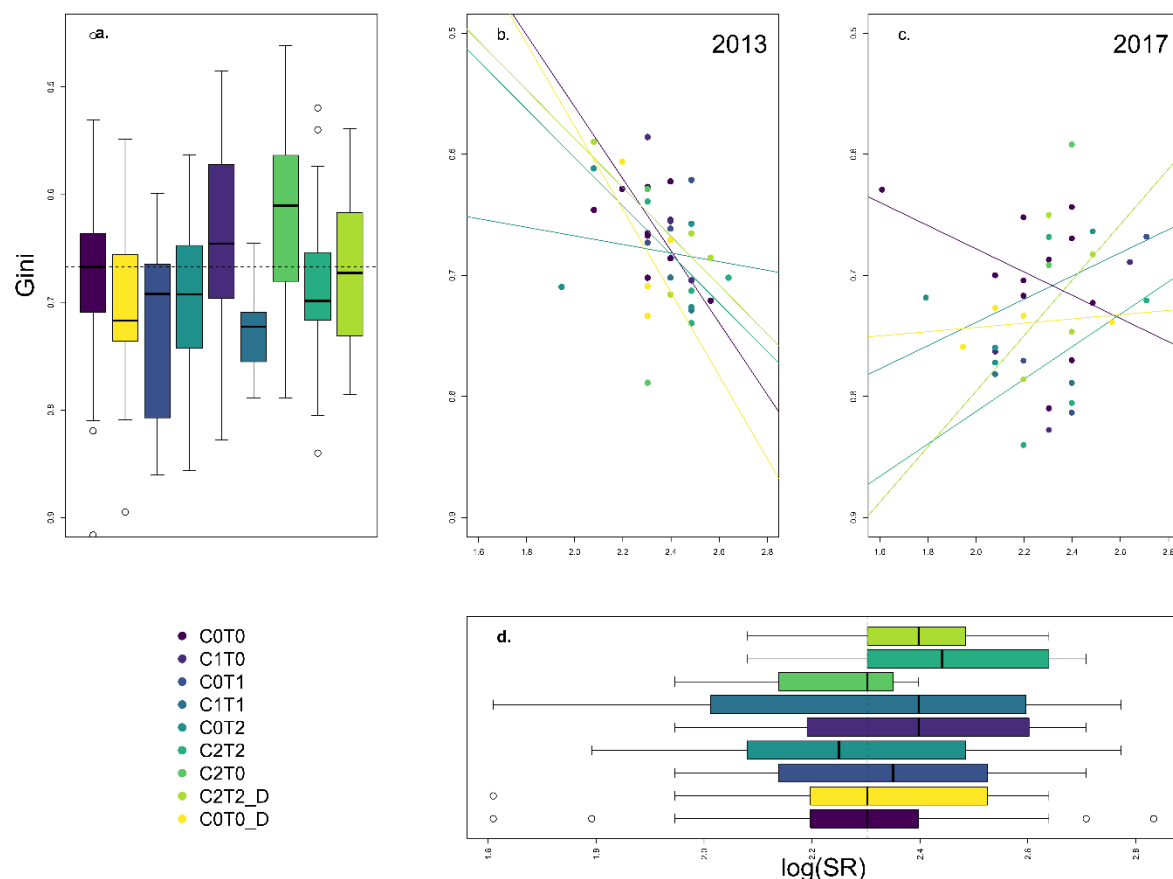
15

392

Figure 2: Treatment differences in **a.** mean evenness, c., and d. richness evenness relationship before reseeding (2013 and 2017) and **d.** mean species richness. Only results from prior to reseeding are shown, but only from plots that were eventually reseeded in 2018, i.e., from years 2013 and 2017. Dashed line in boxplots indicates value of the control (C0T0). Black bars indicate median, and boxes indicate 25% and 75% quantiles. Colors indicate treatments. Treatment codes indicate temperature (T1 = +1.5 °C, T2 = +3°C) and CO_2 (C1 = +150 ppm, T2 = +300 ppm) levels and drought treatment (D = drought). Gini is used as an evenness metric, where 0 indicates complete evenness, and 1 indicates complete dominance. For easier interpretability, all evenness axes in the main figures are flipped, i.e., to display 1 at the bottom of the axis and 0 at the top. Data are from vegetation surveys conducted in 2013 and 2017, prior to reseeding. Note, however, that to avoid post-treatment biases, we only include data from plots that were eventually reseeded as part of the experiment.

16

Treatments affect richness-evenness relationships

We found significant effects of both temperature and CO_2 treatments on the relationship between evenness and richness (RER), but interestingly not always in treatments with significant differences in species richness and evenness in comparison to the control (Tab. 2 and Fig. S7-10). Treatment C2T0 (+300 ppm), C0T1 (+1.5°C) and C0T2 (+3°C) showed significant differences in RER slope before reseeding in comparison to the control, while there was no significant difference in evenness or richness alone (Tab. 2). Additionally, both climate scenarios (C1T1 and C2T2), showed no difference in RER slope in comparison to the control (Fig. 3, c), with the only significant difference arising for the intercept (p-value < 0.05) in C2T2 (+300 ppm, + 3 °C), despite significant differences in evenness (C1T1, C2T2) and species richness (C2T2). Combining these scenarios with drought treatments only resulted in small, non-significant differences in RER in comparison to the control (Fig. 2, d).

While the RER in control plots was positive, the relationship became negative in both the +300 ppm and +150 ppm CO_2 treatments (C1T0, C2T0), with significant differences detected between the +300 ppm (C2T0) vs. control (C0T0) RER slope, as well as between the +300 ppm (C2T0) and the +150 ppm (C1T0) treatment (slope: p-value < 0.05, intercept: p-value < 0.05) (Fig. 3, a and Tab. 2). The temperature treatments (C0T1, C0T2) had similar impacts on RER, though the difference between the control and treatment RER was larger for the +1.5 ° C (C0T1) treatment (slope: p-value < 0.05, intercept: p-value < 0.05) than for the +3°C (C0T2) treatment (intercept: p-value < 0.05), where only the intercept was significantly different from the control (Fig. 2, b). Combining these scenarios with drought treatments only resulted in small, non-significant differences in the RER compared to the control (Fig. 3, d and Tab. 2).

432 **Table 2:** Slopes for the richness evenness relationship (RER) before and after reseeding,

433 values represent model estimates, stars (*) indicate significant difference from control

434 before/after reseeding (C0T0). The significance of differences in RER was identified by

435 comparing the posterior distributions of intercept and slope estimates across the fitted

436 regressions.

437

| Code	CO_2 level	Temperature level	RER Slope *before* reseeding	RER Slope *after* Reseeding	Evenness/ Richness *before* reseeding	Evenness/ Richness *after* reseeding
C0T0	ambient	ambient	- 0.618 (±0.26 SE)	0.926 (±0.31 SE)	0.64/ 10.18	0.70/ 11.25
C0T0_D	ambient	ambient	- 0.107 (±0.54 SE)	1.123 (±0.50 SE)	0.68/ 9.88	0.73/ 10.80
C1T0	+ 150 ppm	ambient	0.684 (±0.76 SE)	**- 0.068*** (±0.55 SE)	0.68/ 11.13	**0.61***/ 11.02
C2T0	+ 300 ppm	ambient	**6.834*** (±3.60 SE)	- 0.262 (±1.09 SE)	0.65/ 9.68	**0.59***/ 8.85
C0T1	ambient	+ 1.5 °C	**1.049*** (±0.74 SE)	0.831 (±0.63 SE)	0.67/ 11.7	**0.77***/ 9.87
C0T2	ambient	+ 3 °C	**0.046*** (±0.36 SE)	1.030 (±0.71 SE)	0.68/ 9.2	0.72/ 10.69
C1T1	+ 150 ppm	+ 1.5 °C	0.157 (±0.96 SE)	0.378 (±0.40 SE)	**0.72***/ 10.8	0.73/ 9.87
C2T2	+ 300 ppm	+ 3 °C	**0.311*** (±0.61 SE)	0.643 (±0.66 SE)	**0.7***/ **11.94***	0.67/ 12.18
C2T2_D	+ 300 ppm	+ 3 °C	- 0.388 (±0.62 SE)	1.338 (±1.09 SE)	0.66/ 9.39	0.69/ 11.59

438
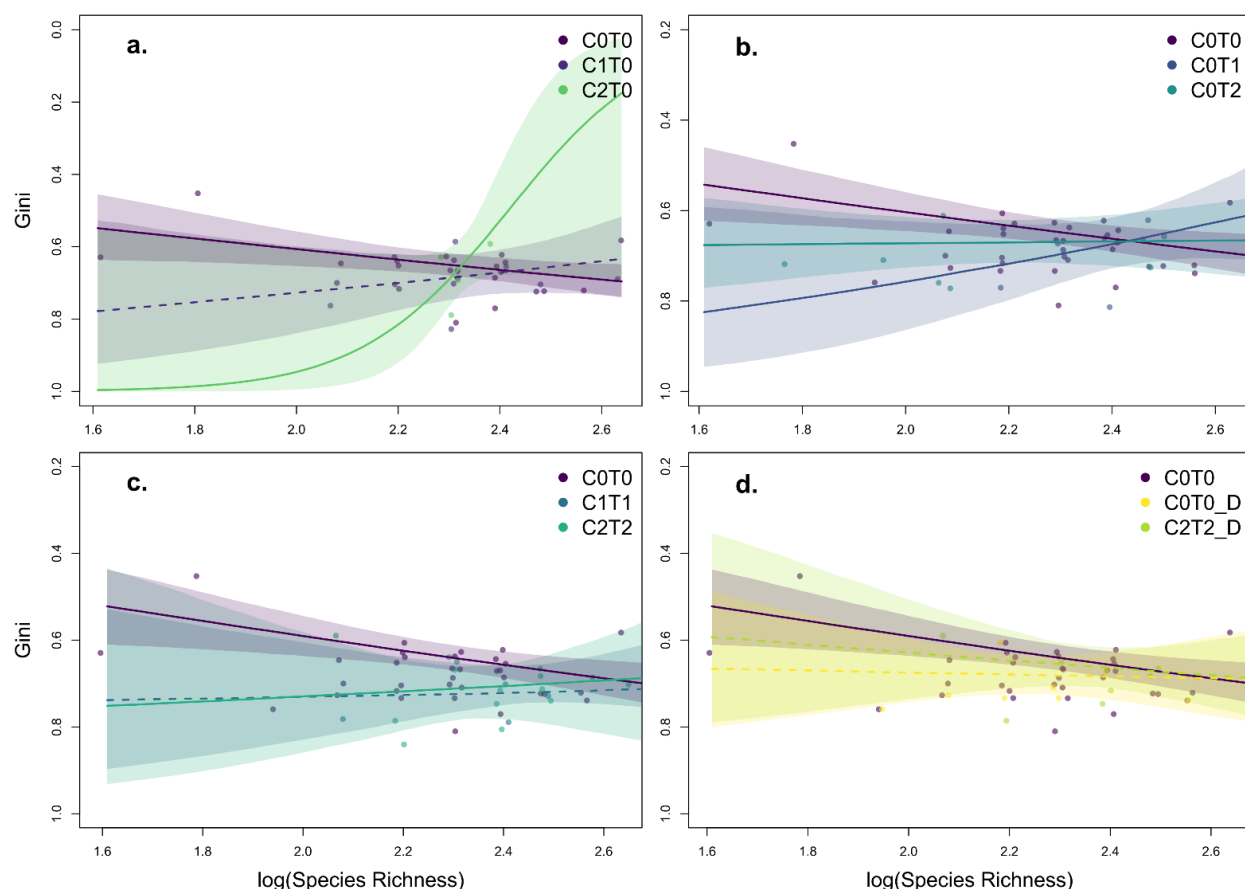
Figure 3: Climate change treatments alter richness-evenness relationships (RER) prior to re-seeding for control plots vs. **a.** CO_2 treatments (C1T0: +150 ppm and C2T0: +300 ppm), **b.** temperature treatments (C0T1: +1.5 °C and C0T2: +3°C), **c.** climate change scenario 1 (C1T1: +150 ppm, + 1.5°C) and 2 (C2T2: +300 ppm and +3°C), and **d.** drought treatments C0T0_D, C2T2_D (implemented only for control and scenario 2 plots). Shaded regions show 95% confidence intervals. Points show single plots; points and lines are colored by treatment level (purple for control, blue for first level, and yellow for second level). Dashed lines indicate treatments with slopes not significantly different from the control (see Fig. 2). Regression structure is described in the data analyses section of the methods. Gini is used as an evenness metric, where 0 indicates complete evenness, and 1 indicates complete dominance. For easier interpretability, all evenness axes in the main figures are flipped, i.e., to display 1 at the bottom of the axis and 0 at the top. Data are from vegetation surveys conducted in 2013 and 2017, prior to reseeding. Note, however, that to avoid post-treatment biases, we only include data from plots that were eventually reseeded as part of the experiment.

19

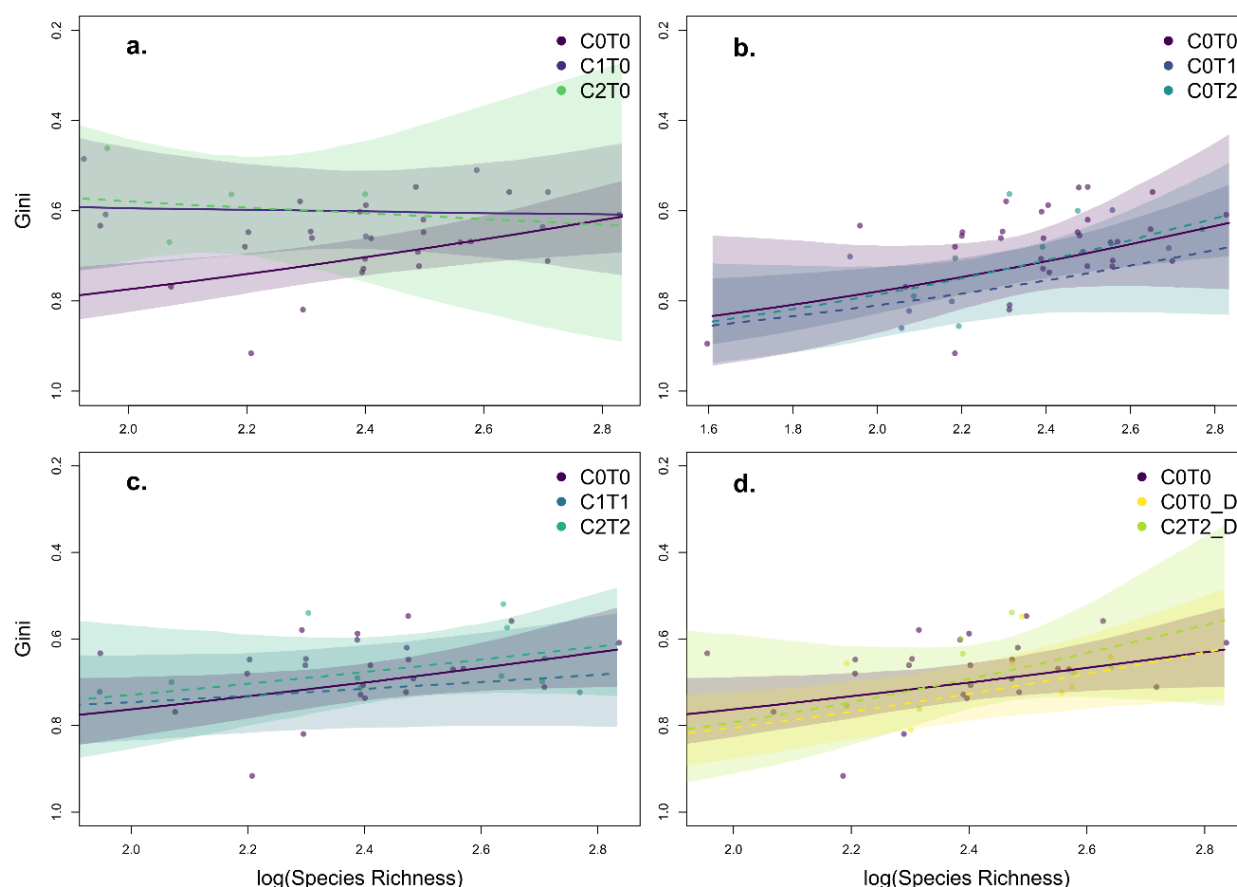455   Reseeding removes differences between treatments

456

Figure 4: Richness-evenness relationship (RER) responses to climate change treatments after reseeding for control plots vs. **a.** CO_2 treatments (C1T0: +150 ppm and C2T0: +300 ppm), **b.** temperature treatments (C0T1: +1.5 °C and C0T2: +3°C), **c.** climate change scenarios 1 (C1T1: +150 ppm, + 1.5°C) and 2 (C2T2: +300 ppm and +3°C), and **d.** drought treatments C0T0_D, C2T2_D (implemented only for control and scenario 2 plots). Points, lines, and intervals are as described in the legend to Fig. 2. Data are from vegetation surveys conducted after reseeding (i.e., post-2017), including data only from reseeded plots.

To test whether reseeding can erase, or at least partially alleviate, the effects of climate change on the RER in our system, we also analyzed the RER in all climate change treatments after reseeding. Reseeding took place in early April 2018, 2020, and 2021 – thus, post-reseeding vegetation surveys are available from 2019 and 2022. There is no clear temporal pattern in the evenness and species richness data, despite the increase in evenness after reseeding in 2018 (Fig. 1, c and d). Additionally, we added year as a categorical fixed effect in our brms models for the RER to control for temporal variation. Recall that the seed mixture used for

20

473   reseeding was identical to the initial seed mixture; therefore, no new species were

474   actively introduced.

475   After reseeding, the RER was positive across almost all control and treatment plots,

476   except for the slight negative RER trends in the CO_2 treatments (Fig. 4a- d). In

477   general, there is only one significant difference between the slope after reseeding

478   between the control and the C1T0 (+150 ppm) treatment, which was significantly

479   lower than in the control plots (Tab. 2).

480   To investigate the differences in evenness and richness separately before and after

481   reseeding, we compared Control (C0T0) and treatment plots. Evenness, but not

482   richness, was significantly higher in the CO_2 treatments (C1T0, C2T0), and

483   significantly lower in the lowest temperature treatment (C0T1: +1.5°C). Interestingly,

484   there again was no significant difference in richness or evenness in the C1T0

485   treatment (+150 ppm) in comparison to the control, despite the significant difference

486   in RER slope (Tab. 2, Fig. 4).

487

488   Interestingly, we found that reseeding had different effects on plots depending on

489   whether they had high or low species richness at the time of reseeding (Fig. 5).

490   Reseeding in control plots (C0T0) seemed to reduce evenness. In the CO_2

491   treatments (C1T0: +150 ppm, C2T0: +300 ppm), low richness plots increased in

492   richness following reseeding, whereas high richness plots lost species, but gained

493   evenness. In contrast, in temperature treatments (C0T1: +1.5°C, C0T2: +3°C),

494   evenness declined after reseeding in high richness plots, with simultaneous species

495   loss in high richness plots and species gains in low richness plots (Fig. 5, b). The

496   scenarios (C1T1: +150 ppm, +1.5°C; C2T2: +300 ppm, +3°C) gained species

497   following reseeding in high richness plots (C2T2) and in low richness plots (C1T1)

498   (Fig. 5c). In contrast to the other treatments, only 2 plots of the drought treatments

499   (C0T0_D: ambient, + drought, C2T2_D: +300 ppm, +3°C, + drought) lost species

500   following reseeding, while most plots gained species regardless of their species

501   richness prior to reseeding (Fig. 5 d). According to these differences, reseeding of

502   plots seemed to reduce differences in the RER among treatments, but did not

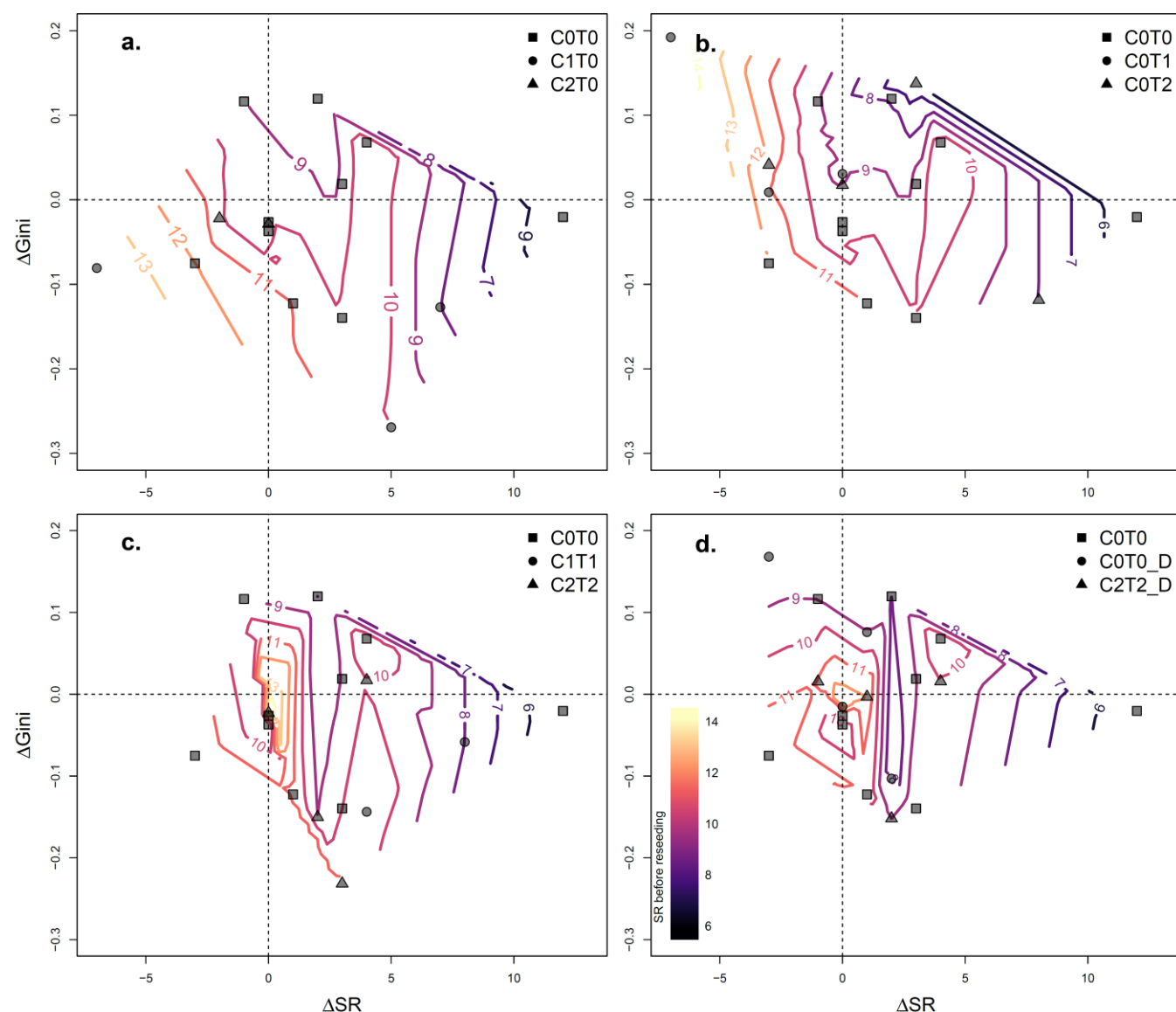503   restore the negative RER observed in the control plots before reseeding.

Figure 5: Reseeding enhances richness in low richness plots and reduces richness in high richness plots. Differences (Δ) in species richness and Gini before (≤2017) and after reseeding (≥2019), relative to plot-level species richness observed prior to reseeding. Dashed lines show no difference (Δ = 0) in species richness or evenness before and after reseeding, and colored contour lines show species richness before reseeding. Points show single plots separated by treatment. Shape indicates treatment levels in **a.** CO_2 treatments (C1T0: +150 ppm and C2T0: +300 ppm), **b.** temperature treatments (C0T1: +1.5 °C and C0T2: +3°C), **c.** climate change scenarios 1 (C1T1: +150 ppm, + 1.5°C) and 2 (C2T2: +300 ppm and +3°C), and **d.** drought treatments C0T0_D, C2T2_D (implemented only for control and scenario 2 plots). Gini is used as an evenness metric, where 0 indicates complete evenness, and 1 indicates complete dominance. Only reseeded plots are included in analyses, with Δ comparisons showing differences in plots from the last survey directly before reseeding, vs. the first survey directly after reseeding.

22

Dominant grass species could cause differences in richness-evenness relationships before and after reseeding.

To examine whether the dominant grass species *Arrhenatherum elatius* could be responsible for the differences in the RER before and after reseeding, we looked at how its cover changed as a function of plot-level species richness (Fig. 6). Overall, we found that the cover of *A. elatius* was higher across all treatments after reseeding (Fig. 6, e and f). In the CO_2 treatments, the cover of *A. elatius* increased in high richness plots and decreased in low richness plots, whereas plot-level richness changed in the opposite direction (Fig. 6, a). The same pattern occurs for evenness and richness before and after reseeding, where high richness plots lost species but gained evenness and low richness plots gained species and decreased in evenness (Fig. 5, a). The temperature treatments (C0T1: +1.5 °C and C0T2: +3 °C) showed similar trends, where high richness plots tended to lose species and gain *A. elatius* cover (Fig. 6, b). In contrast, in the climate change scenarios (C1T1 and C2T2), all plots gained *A. elatius* cover, while also gaining richness, regardless of the richness before reseeding (Fig. 6, c). In the drought treatments (C0T0_D and C2T2_D), 2 plots lost species while gaining *A. elatius* cover (Fig. 6, d).
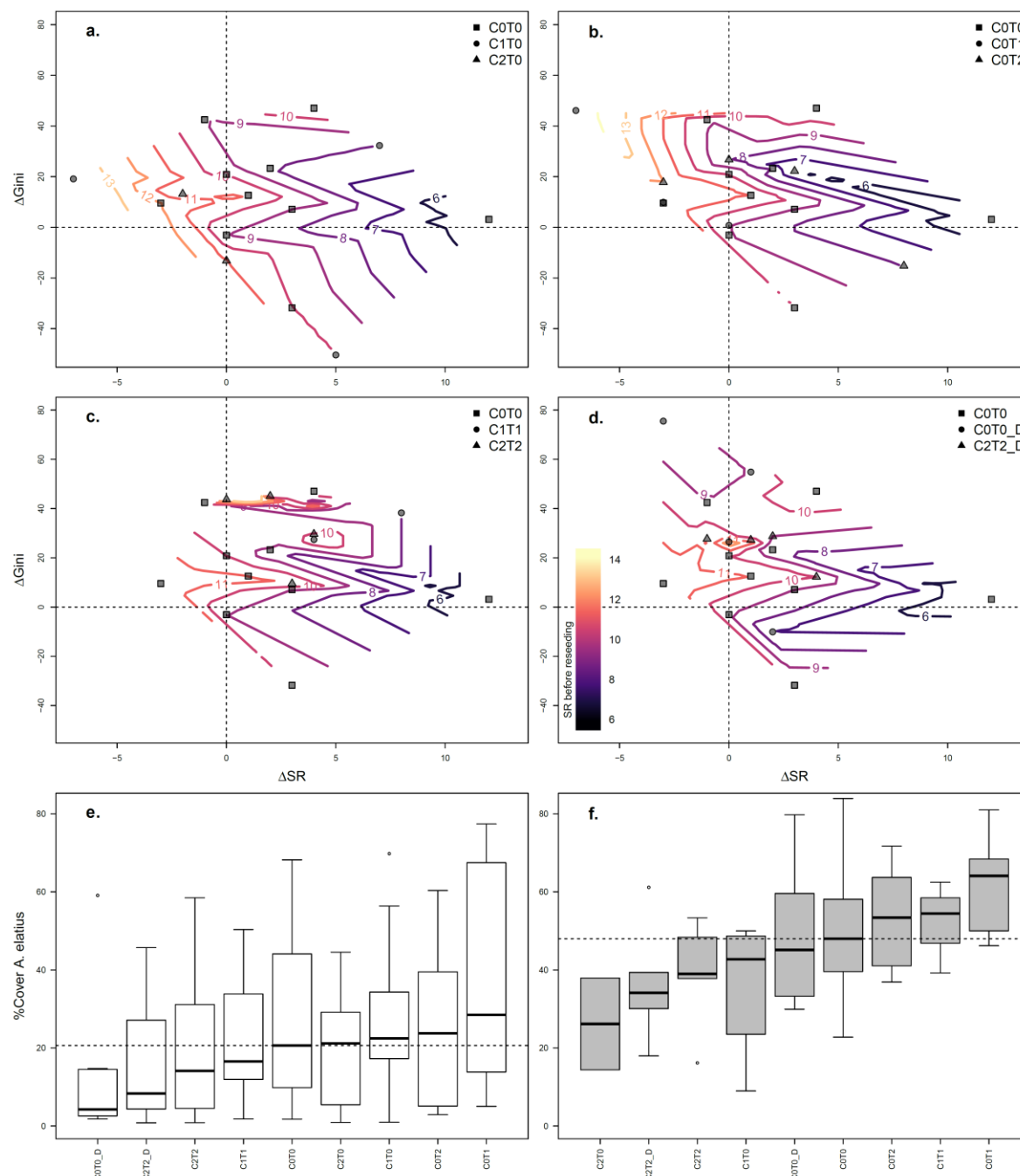
23

Figure 6: Reseeding enhances *A. elatius* %cover. Differences (Δ) in species richness and *A. elatius* %cover before (≤2017) and after reseeding (≥2019), relative to plot-level species richness observed prior to reseeding. Dashed lines show no change in species richness or *A. elatius* cover, and colored contour lines show species richness before reseeding. Gini is used as an evenness metric, where 0 indicates complete evenness. Points show single plots separated by treatment. Shape indicates treatment levels in **a.** CO$_2$ treatments (C1T0: +150 ppm and C2T0: +300 ppm), **b.** temperature treatments (C0T1: +1.5 °C and C0T2: +3°C), **c.** climate change scenarios 1 (C1T1: +150 ppm, + 1.5°C) and 2 (C2T2: +300 ppm and +3°C), and **d.** drought treatments C0T0_D, C2T2_D (implemented only for control and scenario 2

24

545   plots). **e., f.** show %cover of *A. elatius* before and after reseeding in all treatments. The

546   dashed line indicates the median of *A. elatius* cover in control plots. Black bars indicate

547   median, boxes 25% and 75% quantiles. Only reseeded plots are included in analyses, with Δ

548   comparisons showing changes in plots from directly before vs. directly after reseeding.

549   Discussion (1755)

550   Our results show that, in contrast to evenness or richness alone, richness evenness

551   relationships (RERs) are sensitive to community changes in our experiment, as they

552   contain additional information to means or similar approaches of evenness and

553   richness alone. Also, RERs could indicate changes that differ between high and low

554   richness communities. The RER captures changes in the relationship between

555   community diversity and the distribution of relative abundances across the

556   community. Consequently, the RER may be a first sign of changes in communities

557   affected by climate change, as suggested for evenness (Chapin et al. 2000). Plant

558   communities are expected to have negative RERs (Soininen et al., 2012; Zhang et

559   al., 2012; Hordijk et al., 2023), which corresponds to our results in the non-reseeded

560   control. We show that the RER in our experiment differs significantly between

561   treatments and control before reseeding, even without any corresponding differences

562   in richness or evenness. Therefore, RER represents a signal of community change

563   that differs from what can be gleaned from richness and evenness separately.

564   This increased sensitivity is especially important in alpine and subalpine regions, as

565   there can be a lag in species responses to climate change, likely longer than in other

566   ecosystems (Alexander et al. 2018; Rumpf et al. 2019). This potential lag suggests

567   that future changes in affected communities could be substantially larger than those

568   observed thus far. There is evidence that the signs of the RER change with

569   environmental context, trophic level, or taxa. Also, Stirling and Wilsey (2001) showed

570   that observed relationships between richness and evenness differed from

571   combinations of evenness and richness, generated by a neutral model. This

572   indicates that biological processes shape the relationship between richness and

573   evenness.

574   The difference in RER was strongest between temperature treatments and the

575   control, which corresponds to previously reported changes in community

576   composition reported from lowland (Kardol et al.,2010) and alpine grassland

577   ecosystems (Liu et al., 2018). In contrast to our expectations, richness, and

578   evenness did not change significantly, but the slope of the RER in both temperature

579   treatments changed significantly, and even the direction of the RER is positive, in

580   contrast to the negative RER in the non-reseeded control. Other studies from the

581   European Alps found contrasting effects, where increased temperatures only

582   affected plants when treatments were accompanied by drought (Boeck et al., 2016).

583   Like other climate change studies, we found decreased evenness in global change

584   treatments (Kardol et al., 2010), but only in both scenarios, i.e., combinations of

585   increased CO_2 and temperature levels. Also, we found almost no changes in species

586   richness, other than a significant increase in the climate scenario with +300 ppm CO_2

587   and +3°C in temperature. This contrasts with our expectations, where we expected

588   species richness or evenness separately to differ in treatments and controls. The

589   effect of elevated CO_2 and temperature seemed to change the RER in similar ways

590   in comparison to the control, but their combined effects led to a less pronounced

591   relationship between richness and evenness, with only Scenario 2 (+300ppm, 3°C)

592   being significantly different from the control. This result could indicate that CO_2 and

593   temperature interact and at least partly counteract one another's effects on the RER,

594   but not enough to restore the negative RER found in the control. Indeed, some

595   previous studies have found evidence that elevated CO_2 concentrations can

596   ameliorate the effects of temperature increases (Reyes-Fox et al., 2014; Roy et al.,

597   2016) – potentially because higher CO_2 concentrations lead to reduced

598   evapotranspiration, thereby buffering the effects of increased temperature (Slawitsch

599   et al., 2020).

600   The lack of a significant impact of drought treatments on the RER is surprising, and

601   contrasts with some results from other climate change experiments (e.g., White et

602   al., 2014), as well as with our hypotheses. A potential explanation, which matches

603   findings from other managed European grasslands, is that water availability was

604   sufficiently high to prevent drought stress, even within the drought treatments

605   (Hopkins and Del Prado 2007). Indeed, average annual precipitation at our site is

606   particularly high (at 1077 mm/year), and has been increasing with time (see

607   Supplement, Fig. S1). Additionally, recall that in our experiment, drought treatments

608   were implemented as a single, severe event per year, after which re-wetting was

609   applied, as is predicted by climate model forecasts, which predict increased net

26

610 precipitation with more heavy rain events and dry periods (Gobiet et al., 2014). The

611 short "pulse" may have reduced the effects of drought on species richness and

612 evenness relative to those from longer-term treatments in other experiments – e.g.,

613 in the experiment conducted by Kardol et al. (2010), where water content was

614 controlled throughout the duration of the experiment, and the authors found a

615 significant decrease in evenness. Indeed, responses to climate change, especially to

616 drought, seem to differ by local climate and ecosystem properties (Isbell et al., 2015;

617 Boeck et al., 2018).

618

619 Another important result is that high and low richness communities often seem to

620 react in opposite directions to reseeding, a community change that is visible through

621 the richness evenness relationship (RER). This result is probably due to

622 *Arrhenaterum elatius*, which was the dominant grass species in all plots after

623 reseeding, and in most plots even before reseeding. In our experiment, reseeding

624 can be thought of as an active restoration method, which is practiced by farmers

625 already today. Reseeding affected the dominance of *A. elatius*, and therefore

626 seemed to change the direction of the RER. The lowest dominance of *A. elatius*

627 seems to indicate no relationship between evenness and richness, or even a slightly

628 positive RER, while an increase in dominance leads to more negative RERs. All

629 treatments in which *A. eliatus* had high dominance, both before and after reseeding,

630 showed a positive RER, i.e., low richness plots with low evenness and high richness

631 plots with high evenness. Therefore, high dominance of A. elatius prior to reseeding

632 was generally associated with low richness and low evenness in plots, both of which

633 increased after reseeding. In contrast, plots that had high richness prior to reseeding

634 also tended to have low evenness and low dominance of *A. elatius* – but, after

635 reseeding, dominance of *A. elatius* generally increased, while richness and

636 evenness both decreased. In sum, reseeding partially alleviated the differences in

637 the RER between treatments and controls, but failed to fully restore the negative

638 RER found in the controls, as suggested in Fig. 1, e. The only exceptions to this

639 pattern were both CO_2 treatments, where the RER is negative after reseeding,

640 potentially because fewer plots were re-seeded in these treatments (C1T0, +150

641 ppm: n = 3; C2T0, +300 ppm: n = 2). This difference also shows a major problem in

642 assessing the reseeding treatments in our study. Reseeding mainly took place after

643 the occurrence of "pests" (e.g., ants) and was not part of the experimental design.

644   Therefore, the number of reseeded plots differs somewhat among treatments, which

645   can make direct comparisons difficult. Recall again that to avoid potential biases in

646   our main analyses, we always limit comparisons either to plots that have not yet

647   been reseeded (i.e., survey years prior to 2017) or to subsets of data for which all

648   plots were reseeded (i.e., survey years after 2017).

649   Our results from reseeding are in line with recent evidence from animal populations,

650   where captive release is suggested to increase interspecific competition, thereby

651   destabilizing communities (Terui et al. 2023). The results suggest that the large

652   amount of *A. elatius* in the seed mixture used for reseeding (14.9 %, see Table S4)

653   contributes to decreases in plot-level richness and decreases in evenness,

654   especially in high richness communities. This underlines the concerns raised about

655   the ecological risks of intentional release, relocation, or reseeding programs (Araki et

656   al. 2007; Krkosek et al. 2007; Kitada 2014). While most of this evidence is derived

657   from fish, massive releases of plant species also occur in many restoration projects

658   (Laikre et al. 2006) – and the risks that these efforts pose for community diversity,

659   stability, and productivity remain poorly understood. While in our experiment, re-

660   seeding allows low richness communities to gain species, it also appears to drive

661   species loss in high richness communities.

662   The consequences of different RERs are less clear, but this relationship is probably

663   meaningful, as evenness, like richness, is an important contributor to many different

664   ecosystem properties (Kirwan et al. 2007; Hillebrand et al. 2008; Wittebolle et al.

665   2009; Wilsey and Potvin 2000). Also, a previous study has found that RERs seem to

666   mediate the relationship between forest productivity and richness (Hordijk et al.,

667   2023), where in low richness systems, uneven communities are more productive

668   than even ones. In contrast, in high richness systems, even communities are more

669   productive than uneven ones. This underpins the importance of our findings of

670   positive RERs as a result of reseeding or climate, which would indicate that the less

671   productive communities (low richness, high evenness and high richness, low

672   evenness) get replaced by more productive communities (low richness, low

673   evenness and high richness, high evenness) (Fig. 1, b). Therefore, changing RERs

674   could greatly affect the productivity of grassland communities. Also, the stability of

675   ecosystems is suggested to be affected not only by evenness and richness but

676   probably depends on the combination of richness and evenness, as they shape

28

677   different aspects of stability (Hillebrand et al., 2008). As more diverse seed mixtures

678   increase productivity, with corresponding economic benefits in intensively used

679   grasslands (Binder et al. 2018), adjusting evenness accordingly to species richness

680   could further increase these benefits. Taken together, this emphasizes the

681   importance of further investigating the reasons and consequences of different

682   richness evenness relationships (RER).

683   In summary, we provide evidence that 1) climate change alters the richness-

684   evenness relationship (RER) in our grassland communities, disconnected from

685   changes in evenness and richness, and that 2) reseeding can partially alleviate the

686   changes in the RER across all treatments, but does not restore the negative RER of

687   the control. The RER can reveal insights into community responses to climate

688   change, more sensitive than richness or evenness alone. Like our results from the

689   reseeding show, evenness and species richness in communities is especially

690   important to consider before reseeding, because low and high richness plots can

691   react differently to global change drivers and to management, thereby affecting the

692   direction of the RER, with consequences for productivity and stability (Hillebrand et

693   al., 2008; Hordijk et al., 2023.

694   As the effects of reseeding differ for each treatment, the RER could help to better

695   match restoration treatments to global change drivers. Our results suggest that

696   incorporating the RER into management decisions might be important and that

697   carefully chosen seed mixtures could ameliorate the impacts of climate change. Our

698   results show that reseeding with the original seed mixture for buffering biodiversity

699   responses to climate change can lead to less productive meadows by supporting the

700   dominant species. Therefore, a more nuanced approach integrating evenness,

701   richness, and their relation in seed mixtures could be an important step forward to

702   buffer the effects of climate change, not only in intensively used grasslands.

References (48)

Alexander, Jake M.; Chalmandrier, Loïc; Lenoir, Jonathan; Burgess, Treena I.; Essl, Franz; Haider, Sylvia et al. (2018): Lags in the response of mountain plant communities to climate change. In: Global Change Biology 24 (2), S. 563–579. DOI: 10.1111/gcb.13976.

Araki, Hitoshi; Cooper, Becky; Blouin, Michael S. (2007): Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. In: Science (New York, N.Y.) 318 (5847), S. 100–103. DOI: 10.1126/science.1145621.

Binder, Seth; Isbell, Forest; Polasky, Stephen; Catford, Jane A.; Tilman, David (2018): Grassland biodiversity can pay. In: Proceedings of the National Academy of Sciences of the United States of America 115 (15), S. 3876–3881. DOI: 10.1073/pnas.1712874115.

Blowes, Shane A.; Daskalova, Gergana N.; Dornelas, Maria; Engel, Thore; Gotelli, Nicholas J.; Magurran, Anne E. et al. (2022): Local biodiversity change reflects interactions among changing abundance, evenness, and richness. In: Ecology, e3820. DOI: 10.1002/ecy.3820.

Boeck, Hans J. de; Bassin, Seraina; Verlinden, Maya; Zeiter, Michaela; Hiltbrunner, Erika (2016): Simulated heat waves affected alpine grassland only in combination with drought. In: The New phytologist 209 (2), S. 531–541. DOI: 10.1111/nph.13601.

Boeck, Hans J. de; Bloor, Juliette M. G.; Kreyling, Juergen; Ransijn, Johannes C. G.; Nijs, Ivan; Jentsch, Anke; Zeiter, Michaela (2018): Patterns and drivers of biodiversity-stability relationships under climate extremes. In: Journal of Ecology 106 (3), S. 890–902. DOI: 10.1111/1365-2745.12897.

Bürkner, Paul-Christian (2017): brms : An R Package for Bayesian Multilevel Models Using Stan. In: Journal of Statistical Software 80 (1). DOI: 10.18637/jss.v080.i01.

Bütof, Astrid; Riedmatten, Lars R. von; Dormann, Carsten F.; Scherer-Lorenzen, Michael; Welk, Erik; Bruelheide, Helge (2012): The responses of grassland plants to experimentally simulated climate change depend on land use and region. In: Global Change Biology 18 (1), S. 127–137. DOI: 10.1111/j.1365-2486.2011.02539.x.

Chao, Anne; Ricotta, Carlo (2019): Quantifying evenness and linking it to diversity, beta diversity, and similarity. In: Ecology 100 (12), e02852. DOI: 10.1002/ecy.2852.

Chapin, F. S.; Zavaleta, E. S.; Eviner, V. T.; Naylor, R. L.; Vitousek, P. M.; Reynolds, H. L. et al. (2000): Consequences of changing biodiversity. In: Nature 405 (6783), S. 234–242. DOI: 10.1038/35012241.

Clare, David S.; Culhane, Fiona; Robinson, Leonie A. (2022): Secondary production increases with species richness but decreases with species evenness of benthic invertebrates. In: Oikos 2022 (4), e08629. DOI: 10.1111/oik.08629.

Deltedesco, Evi; Keiblinger, Katharina M.; Naynar, Maria; Piepho, Hans-Peter; Gorfer, Markus; Herndl, Markus et al. (2019): Trace gas fluxes from managed grassland soil subject to multifactorial climate change manipulation. In: Applied Soil Ecology 137, S. 1–11. DOI: 10.1016/j.apsoil.2018.12.023.

Eurostat (2020): Share of Main Land Types in Utilised Agricultural Area (UAA) by NUTS 2 Regions.

743 Fussmann, Katarina E.; Schwarzmüller, Florian; Brose, Ulrich; Jousset, Alexandre; Rall,
744 Björn C. (2014): Ecological stability in response to warming. In: Nature Climate Change 4
745 (3), S. 206–210. DOI: 10.1038/nclimate2134.

746 Gobiet, Andreas; Kotlarski, Sven; Beniston, Martin; Heinrich, Georg; Rajczak, Jan; Stoffel,
747 Markus (2014): 21st century climate change in the European Alps--a review (493). Online
748 verfügbar unter
749 https://reader.elsevier.com/reader/sd/pii/S0048969713008188?token=2C460EB8248840AF7
750 74E2D97D8FFB9F189D91A59161EA357B16069B5150214F5DCC94AC9ACB297E72D33E
751 F6ED245C77E&originRegion=eu-west-1&originCreation=20230227135403.

752 Gruner, Daniel S.; Bracken, Matthew E. S.; Berger, Stella A.; Eriksson, Britas Klemens;
753 Gamfeldt, Lars; Matthiessen, Birte et al. (2017): Effects of experimental warming on
754 biodiversity depend on ecosystem type and local species composition. In: Oikos 126 (1), S.
755 8–17. DOI: 10.1111/oik.03688.

756 Herndl, Markus; Pötsch, Erich; Bohner, Andreas; Kandolf, Matthias (2011): Lysimeter als
757 Bestandteil eines technischen Versuchskonzeptes zur Simulation der Erderwärmung im
758 Grünland.

759 Hillebrand, Helmut; Bennett, Danuta M.; Cadotte, Marc W. (2008): Consequences of
760 dominance: a review of evenness effects on local and regional ecosystem processes. In:
761 Ecology 89 (6), S. 1510–1520. DOI: 10.1890/07-1053.1.

762 Hopkins, A.; Del Prado, A. (2007): Implications of climate change for grassland in Europe:
763 impacts, adaptations and mitigation options: a review. In: Grass and Forage Science 62 (2),
764 S. 118–126. DOI: 10.1111/j.1365-2494.2007.00575.x.

765 Hordijk, Iris; Maynard, Daniel S.; Hart, Simon P.; Lidong, Mo; Steege, Hans ter; Liang,
766 Jingjing et al. (2023): Evenness mediates the global relationship between forest productivity
767 and richness. In: Journal of Ecology, Artikel 1365-2745.14098. DOI: 10.1111/1365-
768 2745.14098.

769 Isbell, Forest; Craven, Dylan; Connolly, John; Loreau, Michel; Schmid, Bernhard;
770 Beierkuhnlein, Carl et al. (2015): Biodiversity increases the resistance of ecosystem
771 productivity to climate extremes. In: Nature 526 (7574), S. 574–577. DOI:
772 10.1038/nature15374.

773 Kardol, Paul; Campany, Courtney E.; Souza, Lara; Norby, Richard J.; Weltzin, Jake F.;
774 Classen, Aime T. (2010): Climate change effects on plant biomass alter dominance patterns
775 and community evenness in an experimental old-field ecosystem. In: Global Change Biology
776 16 (10), S. 2676–2687. DOI: 10.1111/j.1365-2486.2010.02162.x.

777 Kirwan, L.; LÜSCHER, A.; SEBASTIÀ, M. T.; Finn, J. A.; COLLINS, R. P.; PORQUEDDU, C.
778 et al. (2007): Evenness drives consistent diversity effects in intensive grassland systems
779 across 28 European sites. In: Journal of Ecology 95 (3), S. 530–539. DOI: 10.1111/j.1365-
780 2745.2007.01225.x.

781 Kitada, Shuichi (2014): Japanese chum salmon stock enhancement: current perspective and
782 future challenges. In: Fisheries Science 80 (2), S. 237–249. DOI: 10.1007/s12562-013-0692-
783 8.

784 Klein, Julia A.; Harte, John; Zhao, Xin-Quan (2004): Experimental warming causes large and
785 rapid species loss, dampened by simulated grazing, on the Tibetan Plateau. In: Ecology
786 letters 7 (12), S. 1170–1179. DOI: 10.1111/j.1461-0248.2004.00677.x.

787 Krkosek, Martin; Ford, Jennifer S.; Morton, Alexandra; Lele, Subhash; Myers, Ransom A.;
788 Lewis, Mark A. (2007): Declining wild salmon populations in relation to parasites from farm
789 salmon. In: Science (New York, N.Y.) 318 (5857), S. 1772–1775. DOI:
790 10.1126/science.1148744.

791 Ladouceur, Emma; Isbell, Forest; Clark, Adam T.; Harpole, W. Stanley; Reich, Peter B.;
792 Tilman, G. David; Chase, Jonathan M. (2023): The recovery of plant community composition
793 following passive restoration across spatial scales. In: Journal of Ecology 111 (4), S. 814–
794 829. DOI: 10.1111/1365-2745.14063.

795 Laikre, Linda; Palme, Anna; Josefsson, Melanie; Utter, Fred; Ryman, Nils (2006): Release of
796 alien populations in Sweden. In: Ambio 35 (5), S. 255–261. DOI: 10.1579/05-a-060r.1.

797 Liu, Huiying; Mi, Zhaorong; Lin, Li; Wang, Yonghui; Zhang, Zhenhua; Zhang, Fawei et al.
798 (2018): Shifting plant species composition in response to climate change stabilizes
799 grassland primary production. In: Proceedings of the National Academy of Sciences of the
800 United States of America 115 (16), S. 4051–4056. DOI: 10.1073/pnas.1700299114.

801 Lorenz, M. O. (1905): Methods of Measuring the Concentration of Wealth. In: Publications of
802 the American Statistical Association 9 (70), S. 209. DOI: 10.2307/2276207.

803 Navas, Marie-Laure; Garnier, Eric; Austin, Michael P.; Viaud, Agnès; Gifford, Roger M.
804 (2002): Seeking a sound index of competitive intensity: Application to the study of biomass
805 production under elevated CO_2 along a nitrogen gradient. In Austral Ecology 27 (4),
806 pp. 463–473. DOI: 10.1046/j.1442-9993.2002.01201.x.

807 Niklaus, P. A.; Leadley, P. W.; Schmid, B.; Körner, Ch. (2001): A LONG-TERM FIELD
808 STUDY ON BIODIVERSITY × ELEVATED CO_2 INTERACTIONS IN GRASSLAND. In
809 Ecological Monographs 71 (3), pp. 341–356. DOI: 10.1890/0012-
810 9615(2001)071[0341:ALTFSO]2.0.CO;2.

811 Peratoner, Giovanni; Pötsch, Erich M. (2019): Methods to describe the botanical composition
812 of vegetation in grassland research. In: Die Bodenkultur: Journal of Land Management, Food
813 and Environment 70 (1), S. 1–18. DOI: 10.2478/boku-2019-0001.

814 Piepho, H.-P.; Herndl, M.; Pötsch, E. M.; Bahn, M. (2017): Designing an experiment with
815 quantitative treatment factors to study the effects of climate change. In: Journal of Agronomy
816 and Crop Science 203 (6), S. 584–592. DOI: 10.1111/jac.12225.

817 Potvin, Catherine; Vasseur, Liette (1997): LONG-TERM CO_2 ENRICHMENT OF A
818 PASTURE COMMUNITY: SPECIES RICHNESS, DOMINANCE, AND SUCCESSION. In
819 Ecology 78 (3), pp. 666–677. DOI: 10.1890/0012-9658(1997)078[0666:LTCEOA]2.0.CO;2.

820 Potvin, Catherine; Chapin, F. Stuart; Gonzalez, Andrew; Leadley, Paul; Reich, Peter; Roy,
821 Jacques (2007): Plant Biodiversity and Responses to Elevated Carbon Dioxide. In Josep G.
822 Canadell (Ed.): Terrestrial Ecosystems in a Changing World. With assistance of Diane E.
823 Pataki, Louis F. Pitelka. Berlin, Heidelberg: Springer (Global Change - the IGBP Ser),
824 pp. 103–112.

825 Pötsch, Erich; Herndl, Markus; Bahn, Michael; Schaumberger, Andreas; Schweiger,
826 Medardus; Kandolf, Matthias et al. (2020): ClimGrass -ein innovatives Freilandexperiment
827 zur Erforschung der Folgen des Klimawandels im Grünland.

828 Ramsier, Dieter; Connolly, John; Bazzaz, Fakhri A. (2005): Carbon dioxide regime, species
829 identity and influence of species initial abundance as determinants of change in stand
830 biomass composition in five-species communities: an investigation using a simplex design
831 and RGRD analysis. In *J Ecology* 93 (3), pp. 502–511. DOI: 10.1111/j.1365-
832 2745.2005.00999.x.

833 Reich, Peter B. (2009): Elevated CO_2 reduces losses of plant diversity caused by nitrogen
834 deposition. In *Science (New York, N.Y.)* 326 (5958), pp. 1399–1402. DOI:
835 10.1126/science.1178820.

836 Reyes-Fox, Melissa; Steltzer, Heidi; Trlica, M. J.; McMaster, Gregory S.; Andales, Allan A.;
837 LeCain, Dan R.; Morgan, Jack A. (2014): Elevated CO_2 further lengthens growing season
838 under warming conditions. In: Nature 510 (7504), S. 259–262. DOI: 10.1038/nature13207.

839 Roy, Jacques; Picon-Cochard, Catherine; Augusti, Angela; Benot, Marie-Lise; Thiery, Lionel;
840 Darsonville, Olivier et al. (2016): Elevated CO_2 maintains grassland net carbon uptake under
841 a future heat and drought extreme. In: Proceedings of the National Academy of Sciences
842 113 (22), S. 6224–6229. DOI: 10.1073/pnas.1524527113.

843 Rumpf, Sabine B.; Hülber, Karl; Wessely, Johannes; Willner, Wolfgang; Moser, Dietmar;
844 Gattringer, Andreas et al. (2019): Extinction debts and colonization credits of non-forest
845 plants in the European Alps. In: Nature communications 10 (1), S. 4293. DOI:
846 10.1038/s41467-019-12343-x.

847 Ryals, Rebecca; Hartman, Melannie D.; Parton, William J.; DeLonge, Marcia S.; Silver,
848 Whendee L. (2015): Long-term climate change mitigation potential with organic matter
849 management on grasslands. In: Ecological Applications 25 (2), S. 531–545. DOI:
850 10.1890/13-2126.1.

851 Samson, Fred; Knopf, Fritz (1994): Prairie Conservation in North America. In: BioScience 44
852 (6), S. 418–421. DOI: 10.2307/1312365.

853 Slodowicz, Daniel; Durbecq, Aure; Ladouceur, Emma; Eschen, René; Humbert, Jean-Yves;
854 Arlettaz, Raphaël (2023): The relative effectiveness of different grassland restoration
855 methods: A systematic literature search and meta-analysis. In: Ecological Solutions and
856 Evidence 4 (2), Artikel e12221. DOI: 10.1002/2688-8319.12221.

857 Smith, Benjamin; Wilson, Bastow J. (1996): A Consumer's Guide to Evenness Indices. In:
858 Oikos May (Vol. 76), pp. 70-82.

859 Soininen, Janne; Passy, Sophia; Hillebrand, Helmut (2012): The relationship between
860 species richness and evenness: a meta-analysis of studies across aquatic ecosystems. In:
861 Oecologia 169 (3), S. 803–809. DOI: 10.1007/s00442-011-2236-1.

862 Stevens, Nicola; Bond, William; Feurdean, Angelica; Lehmann, Caroline E.R. (2022): Grassy
863 Ecosystems in the Anthropocene. In: Annual Review of Environment and Resources 47 (1),
864 S. 261–289. DOI: 10.1146/annurev-environ-112420-015211.

865 Stirling, Gray; Wilsey, Brian (2001): Empirical Relationships between Species richness,
866 Evenness, and Proportional Diversity. In: The American naturalist 158, S. 286–299. DOI:
867 10.1086/321317.

868 Tuomisto, Hanna (2012): An updated consumer's guide to evenness and related indices. In
869 *Oikos* 121 (8), pp. 1203–1218. DOI: 10.1111/j.1600-0706.2011.19897.x.

870 Terui, Akira; Urabe, Hirokazu; Senzaki, Masayuki; Nishizawa, Bungo (2023): Intentional
871 release of native species undermines ecological stability. In: Proceedings of the National
872 Academy of Sciences of the United States of America 120 (7), e2218044120. DOI:
873 10.1073/pnas.2218044120.

874 van Sundert, Kevin; Arfin Khan, Mohammed A. S.; Bharath, Siddharth; Buckley, Yvonne M.;
875 Caldeira, Maria C.; Donohue, Ian et al. (2021): Fertilized graminoids intensify negative
876 drought effects on grassland productivity. In: Global Change Biology 27 (11), S. 2441–2457.
877 DOI: 10.1111/gcb.15583.

878 Veronika Slawitsch; Steffen Birk; Markus Herndl; Erich M Pötsch (Hg.) (2019): Einfluss des
879 Klimawandels auf die Bodenwasserbilanz im inneralpinen Grünland. 21. Alpenländisches
880 Expertenforum.

881 WallisDeVries, Michiel F.; Poschlod, Peter; Willems, Jo H. (2002): Challenges for the
882 conservation of calcareous grasslands in northwestern Europe: integrating the requirements
883 of flora and fauna. In: Biological Conservation 104, S. 265–273.

884 Wang, Hao; Liu, Huiying; Cao, Guangmin; Ma, Zhiyuan; Li, Yikang; Zhang, Fawei et al.
885 (2020): Alpine grassland plants grow earlier and faster but biomass remains unchanged over
886 35 years of climate change. In: Ecology letters 23 (4), S. 701–710. DOI: 10.1111/ele.13474.

887 Wang, Xiao-Yan; Ge, Yuan; Gao, Song; Chen, Tong; Wang, Jiang; Yu, Fei-Hai (2021):
888 Evenness alters the positive effect of species richness on community drought resistance via
889 changing complementarity. In: Ecological Indicators 133, S. 108464. DOI:
890 10.1016/j.ecolind.2021.108464.

891 White, Shannon R.; Bork, Edward W.; Cahill, James F. (2014): Direct and indirect drivers of
892 plant diversity responses to climate and clipping across northern temperate grassland. In:
893 Ecology 95 (11), S. 3093–3103. DOI: 10.1890/14-0144.1.

894 Wilsey, Brian J.; Potvin, Catherine (2000): Biodiversity and ecosystem functioning:
895 Importance of species evenness in an old field. In: Ecology 81 (4), S. 887–892. DOI:
896 10.1890/0012-9658(2000)081[0887:BAEFIO]2.0.CO;2.

897 Wittebolle, Lieven; Marzorati, Massimo; Clement, Lieven; Balloi, Annalisa; Daffonchio,
898 Daniele; Heylen, Kim et al. (2009): Initial community evenness favours functionality under
899 selective stress. In: Nature 458 (7238), S. 623–626. DOI: 10.1038/nature07840.

900 Zavaleta, Erika S.; Shaw, M. Rebecca; Chiariello, Nona R.; Mooney, Harold A.; Field,
901 Christopher B. (2003): Additive effects of simulated climate changes, elevated CO_2, and
902 nitrogen deposition on grassland diversity. In: Proceedings of the National Academy of
903 Sciences of the United States of America 100 (13), S. 7650–7654. DOI:
904 10.1073/pnas.0932734100.

905 Zhang, Hui; John, Robert; Peng, Zechen; Yuan, Jianli; Chu, Chengjin; Du, Guozhen; Zhou,
906 Shurong (2012): The relationship between species richness and evenness in plant
907 communities along a successional gradient: a study from sub-alpine meadows of the
908 Eastern Qinghai-Tibetan Plateau, China. In: PloS one 7 (11), e49024. DOI:
909 10.1371/journal.pone.0049024.